NODULATION AND ACETYLENE REDUCTION BY TWO LEGUMES WITH RHIZOBIA INDIGENOUS TO NORTHERN GREAT BASIN SOILS[1]

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ABSTRACT.— *Medicago sativa* L. and *Hedysarum boreale* Nutt. were grown in the greenhouse on soils representing 27 of the major soil associations of the northern Great Basin. Nodulation of *Medicago sativa* L. by indigenous rhizobia occurred with 25 of the soil associations and of *Hedysarum boreale* Nutt. with 21 of these soil associations. Nitrogen fixation, as indicated by acetylene reduction activity, was greater for *Medicago sativa* L. than for *Hedysarum boreale* Nutt. for most of the soil associations. Multiple regression functions incorporating 49 independent climatic, edaphic, and vegetation variables failed to predict acetylene reduction activity with satisfactory precision.

Forage yield and quality have been increased on some range sites by including legumes in reseeding mixtures (Rumbaugh et al. 1982) or by interseeding them into existing vegetation (Lorenz 1982). Alfalfa (*Medicago sativa* L.) and yellow-blossom sweet-clover (*Melilotus officinalis* L.) can maintain satisfactory stand densities by reseeding on some range sites (Nichols and Johnson 1969, Rumbaugh 1982). Although legume seeds can be inoculated with selected, highly efficient nitrogen-fixing strains of *Rhizobium* species prior to planting, the fate of the bacteria has not been determined in arid and semiarid range ecosystems. *Rhizobium meliloti* Dang. strains considered to have potential for inoculant production differed markedly in regard to their competitive abilities on *M. sativa* (Van Rensburg and Strijdom 1982). Not all the strains identified as the better competitors in autoclaved soils were able to satisfactorily nodulate alfalfa plants in a South African field soil containing an established population of *R. meliloti*. Introduced strains of bacteria added to some soils were destroyed rapidly by antagonistic organisms (Katznelson 1940, Waksman and Woodruff 1940). Numbers of *R. meliloti* in alfalfa hay fields decline with increasing age of stands (Barber 1980). Thus, rangeland legumes may be dependent upon indigenous *Rhizobium* populations for inoculation and nitrogen fixation at the time they are first planted or in later generations if they are capable of reseeding.

The objectives of our study were to determine (1) whether or not soils of the northern Great Basin contained indigenous *Rhizobium* strains capable of nodulating *Hedysarum boreale* Nutt. and *M. sativa*, (2) the effectiveness of such strains for nitrogen fixation as indicated by acetylene reduction activity, and (3) the usefulness of easily measured or recognized climatic, edaphic, and vegetative factors for predicting the presence or absence of effective *Rhizobium* populations in rangeland soils of the study area.

MATERIALS AND METHODS

Soil samples were collected during 7 to 12 June 1982 from 85 sites representing 27 of the major soil associations of the northern Great Basin (Table 1). Collection sites (Fig. 1) were located and identified with the aid of soil association maps and descriptions (Wilson et al. 1975). A 2-kg soil sample from the upper 15 cm of the profile was extracted from 5 areas at each site. The five samples from each site were bulked, placed in a polyethylene bag, sealed, labeled, and returned to the laboratory for pH measurement and subsequent refrigeration. Sites were characterized as being cropland or noncropland and the dominant native or introduced plant species were identified. The mean annual precipitation and the summer and annual soil temperatures for each association were also recorded (Wilson et al. 1975).
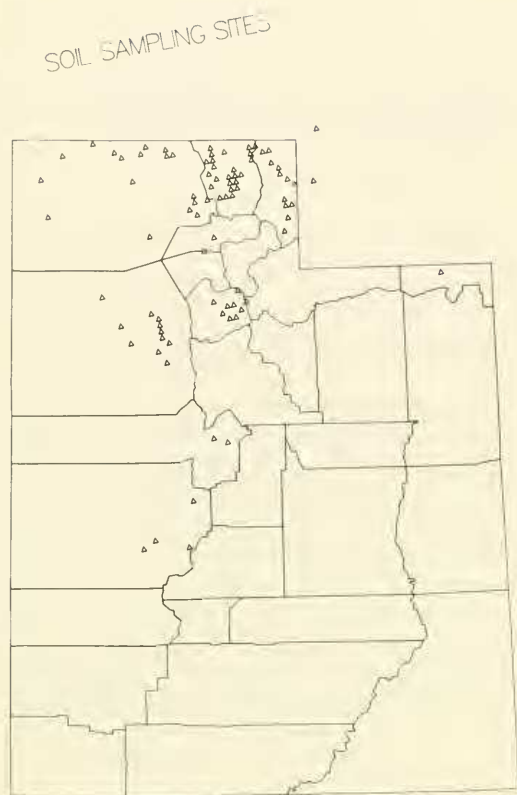
SOIL SAMPLING SITES

Fig. 1. Approximate locations of the 85 soil sampling sites, mostly within the state of Utah.

An experimental population of northern sweetvetch (*H. boreale* Nutt.), which is native to the study region, and 'Spredor 2' alfalfa, an introduced species widely cultivated throughout the Great Basin, were used as macrosymbiont legume hosts.[3] Seeds were mechanically scarified, surface sterilized by immersion in 95% ethyl alcohol for 15 minutes (Jing et al. 1982), and germinated in sterile plastic boxes containing absorbent blotters wetted with tap water. One-week old seedlings were transplanted the first week of July into previously unused, chlorine-treated plastic containers (3.8 cm diameter at the top and tapered over the 21 cm length to a 2.5 cm diameter at the bottom). These containers were filled with soils of the 85 samples that had been screened for pebbles and detritus particles larger than approximately 5 mm di-

ameter. Plants of the two species were grown in the greenhouse in two adjoining locations, with no supplemental lighting. Experimental designs were randomized complete blocks with four replications each. During 27 to 29 September 1982, the plants were removed from the containers and the roots gently washed over fine-meshed screens to remove the soil particles without dislodging the nodules. The shoots of the plants were excised, oven dried, and weighed. Intact roots and attached nodules were used to measure acetylene reduction activity. The procedures followed were similar to those previously described by Johnson and Rumbaugh (1981) except that the intact root systems were incubated one hour in 60-cc plastic syringes. Oven-dry root and nodule weights and nodule numbers were subsequently obtained for each plant. Data were analyzed by analysis of variance, chi-square, and multiple regression.

RESULTS AND DISCUSSION

Nodulation

Fifty-five percent of the alfalfa plants had one or more nodules on their roots, whereas only 32% of the sweetvetch plants were nodulated (Table 2). Despite the fact that sweetvetch is native to the northern Great Basin area and alfalfa is not, indigenous rhizobia were able to nodulate alfalfa more frequently than sweetvetch. Although the absolute nodulation frequencies varied depending upon whether or not the soil collection sites had been cropped, on both cropland and noncropland, alfalfa was nodulated more often than sweetvetch. Twenty-two of the 85 soils samples were from sites currently being used for crop production. On cropland, 68% of the alfalfa and 39% of the sweetvetch plants were nodulated. On noncropland, corresponding frequencies were 53% for alfalfa and 31% for sweetvetch. In both cases the chi-square tests of homogeneity between species were highly significant ($P < 0.01$).

All alfalfa plants grown in the soil samples from associations 33, 35, 45, 50, and 67 were

Table 1. Soil description, dominant species in climax vegetation, and number of sites sampled and tested for each of 27 soil associations.[*]

Association number	Soils	Soil description	Dominant species in climax vegetation[**]	Number of sites sampled
1	Argic Cryoborolls–Pachic Cryoborolls–Cryic Paleborolls Association	High mountain loams and stony loam	Bigtooth maple, slender wheatgrass, quaking aspen, blue wildrye, Douglas fir	15
9	Lithic Argiborolls–Rock outcrop–Typic Argiborolls Association	Mountain loams and mountain gravelly and stony loams	Gambel oak, birchleaf mountain mahogany, mountain brome, bearded wheatgrass	1
21	Typic Argixerolls–Cumulic Haplaquolls Association	Mountain loams, mountain stony loam, upland stony loam, and wet meadow soils	Gambel oak, bearded wheatgrass, bluebunch wheatgrass, big sagebrush, tufted hairgrass, sedges	5
22	Typic Argixerolls–Typic Haploxerolls Association	Mountain loams, mountain stony or gravelly loams, and mountain stony clay soils	Gambel oak, bluebunch wheatgrass, slender wheatgrass, basin wildrye	5
23	Calcic Haploxerolls–Calcic Argixerolls Association	Mountain or upland loams and stony loams	Bluebunch wheatgrass, basin wildrye, big sagebrush, black sagebrush, shadscale	2
24	Lithic Haploxerolls–Typic Haploxerolls Association	Mountain loam, mountain stony, gravelly, or shallow loams	Bluebunch wheatgrass, Gambel oak, curlleaf mountain mahogany, antelope bitterbrush	6
25	Pachic Argixerolls–Typic Argixerolls–Calcic Argixerolls Association	Mountain loams and mountain gravelly or stony loams	Bluebunch wheatgrass, bearded wheatgrass, Gambel oak, basin wildrye, big sagebrush	1
26	Calcic Argixerolls–Calcic Haploxerolls Association	Cropland		5
27	Typic Calcixerolls–Calcic Argixerolls Association	Cropland		2
28	Aquic Calciustolls–Typic Calciaquolls–Fluvaquentic Haplustolls Association	Cropland		7
29	Aridic Calcic Argixerolls–Aridic Haploxerolls Association	Upland loams and upland stony loam	Bluebunch wheatgrass, Utah juniper, antelope bitterbrush	1
30	Lithic Argixerolls–Aridic Haploxerolls–Aridic Calcixerolls Association	Upland loam and upland stony or shallow loams	Bluebunch wheatgrass, Utah juniper, big sagebrush	1
31	Aridic Calcixerolls–Xerollic Calciorthids Association	Upland loam and upland stony loam	Bluebunch wheatgrass, black sagebrush, big sagebrush, antelope bitterbrush	2

[*]Adapted from Wilson, et al. 1975. Soils of Utah.
[**]See Appendix for a listing of the scientific names of these plant species.

Table 1 continued.

Association number	Soils	Soil description	Dominant species in climax vegetation[**]	Number of sites sampled
33	Aridic Calcic Argixerolls–Aridix Petrocalcic Palexerolls Association	Upland loam, upland stony loam, and upland shallow hardpan soils	Bluebunch wheatgrass, Utah juniper, black and big sagebrush, antelope bitterbrush	1
34	Aridic Calcixerolls–Xerollic Calciorthids Association	Upland loam and upland stony and gravelly loams	Bluebunch wheatgrass, big sagebrush, Utah juniper	2
35	Ustic Torrifluvents–Borollic Calciorthids Association	Upland loam or upland stony loams	Bluebunch wheatgrass, big sagebrush, antelope bitterbrush	1
39	Ustollic Haplargids–Ustollic Calciorthids Association	Semidesert loam and semidesert stony hill soils	Bluebunch wheatgrass, Indian ricegrass, needle and thread, big sagebrush	1
43	Aquic Calciorthids–Aquic Ustifluvents Association	Wet or semiwet meadows and semiwet stream bottoms	Sedges, tufted hairgrass, slender wheatgrass bitterbrush	2
44	Xerollic Calciorthids–Xeric Torriorthents Association	Semidesert loam and semidesert gravelly loam	Bluebunch wheatgrass, big sagebrush, black sagebrush	5
45	Xerollic Calciorthids–Xerollic Paleorthids Association	Upland loam, semidesert shallow or gravelly loams, and semidesert shallow hardpan soils	Bluebunch wheatgrass, big sagebrush, Utah juniper	1
47	Xerollic Haplargids–Xerollic Calciorthids Association	Upland or semidesert, semidesert silt or limy, and upland stony loams	Bluebunch wheatgrass, big sagebrush, black sagebrush	7
48	Xeric Torrifluvents–Xerollic Calciorthids Association	Upland or semidesert, semidesert silt or limy, and upland stony loams	Bluebunch wheatgrass, big sagebrush, bottlebrush squirreltail	4
50	Lithic Xerollic Calciorthids–Xerollic Calciorthids Association	Semidesert shallow or limy loams	Bluebunch wheatgrass, black sagebrush, big sagebrush, bottlebrush squirreltail	1
60	Typic Natrargids–Xerollic Natrargids–Typic Calciorthids Association	Semidesert or desert salt and alkali flats and bench soils	Winterfat, shadscale, greasewood, Nuttall saltbush	2
62	Typic Natrustalfs–Typic Natrquolls Association	Semidesert alkali flats and bottoms and salt meadow soils	Bottlebrush squirreltail, greasewood, shadscale, western wheatgrass, Nuttall saltbush	5
67	Ustic Torripsamments Association	Upland sands	Utah juniper, pinyon pine, greenleaf manzanita, big sagebrush	1
71	Playas			2

[*]Adapted from Wilson, et al. 1975. Soils of Utah.
[**]See Appendix for a listing of the scientific names of these plant species.

nodulated. Similarly, all plants of sweetvetch grown on soils of associations 25 and 35 were nodulated. All of these soils except for association 67 were mountain upland, or semi-desert loams supporting growth of bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Smith) and various sagebrush species (*Artemisia*) as dominant components of

the climax vegetation. Even soil association 67, which is an upland sand, has big sagebrush (*Artemisia tridentata* Nutt.) as a dominant species in the climax vegetation. However, 5 of the 6 associations in which either legume was not nodulated also were loam soils supporting populations of bluebunch wheatgrass and big sagebrush. Although Hely and Brockwell (1962) noted that *R. meliloti* populations were positively correlated to density of native grass species in Australia, this pattern was not apparent in soils of the northern Great Basin.

Soil pH ranged from 6.1 to 8.5 and averaged 7.3 in the 85 soil samples used in our study. Even at the lowest pH, 50% of the plants of each of the two macrosymbionts were nodulated. Soil pH can greatly affect population levels of rhizobia. For example,

Sagardoy (1981) found that much of the variation in number of *R. meliloti* in soils near Buenos Aires was dependent on soil pH. Barber (1980), Nutman and Ross (1970), and Rice et al. (1977) also reported that hydrogen ion activity could be a major factor restricting the number of rhizobia in soils. In our study, correlation of pH with nodule number per alfalfa plant was $r = 0.08$ and with nodule dry weight, $r = 0.03$. Coefficients for sweetvetch were of similar magnitude, with $r = 0.09$ and $r = -0.01$ for nodule number and dry weight, respectively. The differences in the results of these studies probably were due to the lower pH values of the soils they studied compared to those of the Great Basin.

Sagardoy (1981) found that 79 of the 86 soil samples he investigated contained alfalfa root-nodule bacteria, and about 16% of the

TABLE 2. Frequency of nodulation of two legumes grown on soils from 27 major soil associations of the northern Great Basin.

Independent variable	No. of plants	Avg. pH	Frequency of nodulation (%)		Probability of homogeneity between species (%)
			Hedysarum boreale	*Medicago sativa*	
SPECIES	678	7.29	32	55	0°
LAND USE					
Cropland	111	7.47	39	68	1
Noncropland	567	7.26	31	53	0
SOIL ASSOCIATIONS					
1	120	6.43	18	47	0
9	8	7.82	25	75	49
21	16	7.41	0	12	100
22	40	7.25	55	50	100
23	16	6.92	50	62	100
24	48	7.40	58	54	100
25	8	6.90	100	50	43
26	41	7.44	30	62	8
27	16	7.74	38	50	100
28	55	7.64	36	48	51
29	8	7.30	50	25	100
30	8	7.56	0	0	100
31	16	7.09	25	75	13
33	8	7.82	0	100	3
34	16	7.36	88	75	100
35	8	7.93	100	100	100
39	8	7.32	0	50	43
43	16	7.08	0	50	8
44	39	7.57	55	53	100
45	8	7.61	0	100	3
47	56	7.26	11	54	0
48	32	7.87	38	56	48
50	8	7.01	50	100	43
60	15	7.76	12	71	4
62	40	7.91	20	65	1
67	8	7.53	25	100	14
71	16	7.49	38	38	100

*Probability of corrected chi-square or Fisher's exact 2 tailed test values.

fields had more than 1,000 rhizobia per gram of soil. In our study, nodulation of alfalfa completely failed in only one of the 85 soil samples (1%) and nodulation of sweetvetch in only 8 of the samples (9%). Rhizobia capable of infecting these two legumes apparently were present in both crop and noncropland throughout most of the geographic region represented by the soils sampled. This was quite different than the results reported by Mahler and Wollum (1982) in their investigation of the seasonal variation of *Rhizobium meliloti* in the more acidic soils of alfalfa hay and cultivated fields in North Carolina. In that state a major problem encountered with alfalfa establishment was described as due to the apparent lack of an effective indigenous soil *R. meliloti* population in fields without a previous alfalfa history.

Statistically significant differences ($P<0.05$) in frequency of nodulation of the two legumes were detected in 6 of the 27 soils associations tested (Table 2). Tests of homogeneity with probabilities of less than 5% were found for associations 1, 33, 45, 47, 60, and 62. In each instance the nodulation rate of alfalfa exceeded that of sweetvetch. The biological basis for the lack of homogeneity could not be positively related to cropping history, pH, soil association, or climax vegetation.

Alfalfa plants had more than twice as many, but significantly ($P<0.05$) smaller, nodules than sweetvetch plants (Table 3). Whenever the legumes were grown on soils of association 35, they had considerably more nodules than when grown on any of the other

soil associations. Association 35 was represented by only one sample collected near Manila, Utah. The upland loam soil at that site supported growth of juniper trees (*Juniperus osteosperma*), big sagebrush (*Artemisia tridentata*), and a native legume (*Astragalus* sp.). The site also had a 10% slope to the south and was located at 1750 m elevation, but appeared very similar to a number of the other collection sites with soils that resulted in much lower numbers of nodules on both legumes.

Acetylene Reduction

Although the alfalfa plants had less shoot, root, and nodule biomass than sweetvetch plants, they exhibited approximately 30% higher acetylene reduction rates (Table 3). The difference was statistically significant ($P<0.05$). The overall mean for specific nodule activity for acetylene reduction as indicated by the amount of ethylene produced per hour per gram of nodule dry weight of alfalfa was more than six times higher than that for sweetvetch. The rate for alfalfa exceeded that for sweetvetch on 24 of the 27 soil associations. This supports previous observations by Johnson and Rumbaugh (1981) that acetylene reduction activity by alfalfa exceeded that of most other legumes grown in the intermountain area.

The relationships of acetylene reduction activity to shoot biomass of the two legumes when grown on each of the 27 soil associations were quite similar (Fig. 2). With few exceptions, sweetvetch was more responsive

TABLE 3. Means and ranges of plant weight and acetylene reduction, $N_2[C_2H_2]$, characteristics of legumes grown on soils representing 27 major soil associations of the northern Great Basin. The ranges are enclosed in parenthesis and are extremes of means for the 27 associations.

	Species	
Variable	*Hedysarum boreale*	*Medicago sativa*
Plant weight (mg)		
Shoot	81 (14–128)°°	70 (20–101)°°
Root	102 (12–172)°°	83 (18–152)°°
Nodules	2.9 (0.0–14.2)°°	1.2 (0.0–3.8)°
Total	186 (26–284)°°	159 (38–256)°°
No. of nodules/plant	2.5 (0.0–40.8)°°	5.8 (0.0–17.5)
Acetylene reduction activity		
Plant (μ moles/h)	0.06 (0.00–0.21)°°	0.08 (0.00–0.26)°
Nodules (μ moles/h/g)	6 (0–22)°	38 (0–94)°

°,°°Differences among means of the 27 associations within species were significant with $P<0.05$ and $P<0.01$, respectively.
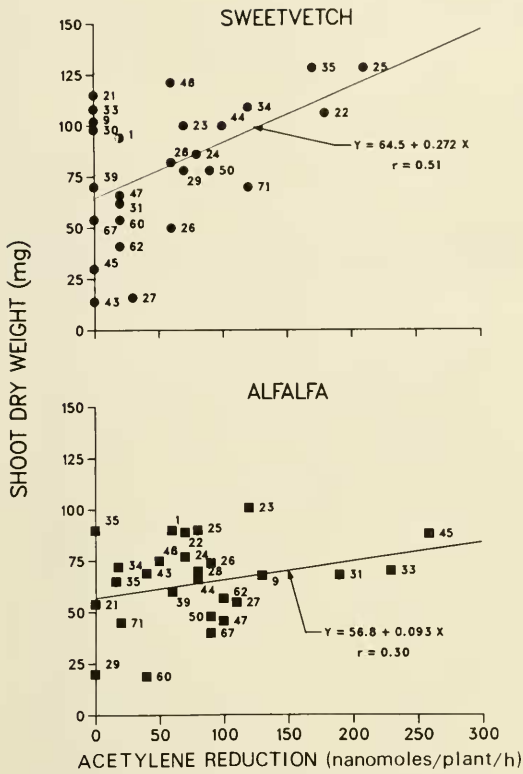
Fig. 2. Relationships of shoot weights to acetylene reduction activities of sweetvetch and alfalfa grown on soils of 27 major associations. See Table 1 for identification of the associations represented by the points and numbers.

collection site was the single most important predictor of acetylene reduction by alfalfa. Similarly, the presence or absence of juniper trees was the single most important predictor of acetylene reduction by sweetvetch. It is highly probable that most wheat fields in northern Utah have been used to produce alfalfa at some time. Sweetvetch commonly occurs in association with juniper in natural stands. Although considerable redundancy in the information content of the independent variables used for prediction was anticipated, the magnitude of the multiple correlation coefficients was lower than expected, with values of 0.46 and 0.50 for whole plant and specific nodule activities, respectively, of alfalfa, and 0.48 and 0.46 for sweetvetch. Although complete nodulation failure with both legumes was observed with only one of the soil associations, nitrogen fixation rates (as indicated by acetylene reduction) could not be predicted very accurately. Also, the predictive functions for alfalfa were quite different than those for sweetvetch. Rank correlation coefficients for the order of entry of the independent variables into the regression equations for the two legumes were $r_s = -0.09$ and $r_s = 0.03$ for whole plant and specific nodule activities, respectively.

Conclusions

Almost all the major soil associations of northern Utah and presumably of the northern Great Basin contain indigenous rhizobia populations of appropriate types and numbers to nodulate *H. boreale* and *M. sativa*. Nitrogen fixation (acetylene reduction activity) by these legumes varied significantly ($P < 0.05$) when grown in the different soils with their respective indigenous rhizobia. These activity levels could not be accurately predicted using any combination of the 49 climatic, edaphic, and vegetation variables included in this study.

than alfalfa to increased reduction, but the relative positions of points representing the associations were much alike. Exceptions could be detected. In an example of the exceptions, soil association 43, a group of aquic calciorthids and aquic ustifluvents, supported growth of alfalfa much better than growth of sweetvetch, although acetylene reduction was zero or low for both kinds of plants. Such differences may be related to differential nutritional demands or susceptibility to soil-borne pathogens.

Stepwise forward multiple regression functions predicting whole plant and specific acetylene reduction activities explained about 25% of the observed variation in the dependent variables. Each function included 7 quantitative and 42 dichotomous independent variables. Activities of the two legume species were predicted with approximately equal precision. The presence or absence of wheat (*Triticum vulgare*) growing at the soil

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APPENDIX

Scientific names of the plant species listed
in Table 1 are the following: Antelope bitter-
brush (*Purshia tridentata* [Pursh] DC.), Basin
wildrye (*Leymus cinereus* [Scribn. & Merr.]
A. Love), Bearded wheatgrass (*Elymus sub-
secundus* [Link] A. & D. Love), Big sage-
brush (*Artemisia tridentata* Nutt.), Bigtooth
maple (*Acer grandidentatum* Nutt.), Birchleaf
mountain mahogany (*Cercocarpus betuloides*
Nutt.), Black sagebrush (*Artemisia nova* A.
Nels.), Blue wildrye (*Elymus glaucus* Buckl.),
Bluebunch wheatgrass (*Elytrigia spicata*
[Pursh] D. R. Dewey), Bottlebrush squirrel-
tail (*Elymus elymoides* [Raf.] Swezey), Curl-
leaf mountain mahogany (*Cercocarpus ledi-
folius* Nutt.), Douglas fir (*Pseudotsuga
menziesii* [Mirb.] Franco), Gambel oak
(*Quercus gambelii* Nutt.), Greasewood (*Sar-
cobatus vermiculatus* [Hook.] Torr.), Green-
leaf manzanita (*Arctostaphylos patula*
Greene), Indian ricegrass (*Oryzopsis hyme-
noides* [Roem. & Schult.] Ricker), Mountain
brome (*Bromus marginatus* Nees ex Steud.),
Needle and thread (*Stipa comata* Trin. &
Rupr.), Nuttall saltbush (*Atriplex nuttallii* H.
& C.), Pinyon pine (*Pinus edulis* Engelm.),
Quaking aspen (*Populus tremuloides* Michx.),
Sedges (*Carex* spp.), Shadscale (*Atriplex con-
fertifolia* [Torr. & Frem.] S. Wats.), Slender
wheatgrass (*Elymus trachycaulus* [Link]
Gould ex Shinners), Tufted hairgrass (*Des-
champsia caespitosa* [L.] Beauv.), Utah juni-
per (*Juniperus osteosperma* [Torr.] Little),
Western wheatgrass (*Pascopyrum smithii*
[Rydb.] Love), and Winterfat (*Ceratoides la-
nata* [Pursh] J. T. Howell).